

PHYLOGENETIC ANALYSIS OF *CYANOPHRYS* CLENCH, A SYNOPSIS OF ITS SPECIES, AND THE POTENTIALLY THREATENED *C. BERTHA* (JONES) (LYCAENIDAE: THECLINAE: EUMAEINI)

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Abstract.—A species level phylogenetic analysis of *Cyanophrys* Clench was performed using 14 characters of the frons, wing venation, wing shape, androconia, and genitalia. There were 15 most parsimonious cladograms, and a successive weighting iteration resulted in three of these 15. *Cyanophrys* is characterized in this paper by two hypothesized synapomorphies (an expanded hindwing anal lobe that is tan-brown and a pair of dorsal brush organs), and adults can be readily identified in the field. *Cyanophrys* has been divided into *Plesiocyanophrys* K. Johnson, Eisele and MacPherson, *Apophrys* K. Johnson and Le Crom, *Antephrys* K. Johnson, Eisele and MacPherson, *Mesocyanophrys* K. Johnson, and *Cyanophrys* (as delimited in Johnson and Le Crom 1997a), but only the monotypic *Antephrys* is monophyletic on the most parsimonious cladograms. A synopsis of *Cyanophrys* species includes notes on their distribution, habitat, identification, nomenclature, larval food plants, and male behavior. *Cyanophrys berthae*, which occurs in moist evergreen and seasonally deciduous forests in the mountains of southern Brazil from 800 to 1,400 m elevation, has been proposed for threatened status. It is “cladistically distinct” (*sensu* Vane-Wright et al. 1991) in that its sister is a lineage of five montane species or seven primarily lowland species.

Key Words: *Callophrys*, phylogeny, venation, genitalia, androconia, brush organs

Generic taxonomy of the primarily Neotropical *Cyanophrys* Clench (Theclinae: Eumaeini) has been unstable (Robbins 2004b). Clench (1961) described it as a subgenus of the Holarctic *Callophrys* Westwood, but since 1993, *Cyanophrys* has been divided into five genera and subgenera, primarily on the basis of differences in genitalia and color of the frons (Johnson et al. 1993, Johnson and Le Crom 1997a).

While most of the 16 *Cyanophrys* species are common and widespread, the Brazilian *C. berthae* (Jones) is exceedingly rare and has been proposed for “vulnerable” status

(Brown 1993, Brown and Freitas 2000 and references therein, Otero et al. 2000). More recently, it has been listed as “almost threatened” (Mielke and Casagrande 2004). Little is known about *C. berthae*, and it is unclear which species, or group of species, is its closest relative. Such information might provide clues to its biology. Further, phylogenetic position is a factor to be considered in assessing the status of threatened species (Vane-Wright et al. 1991).

The first purpose of this paper is to assess the monophyly of the genera and subgenera into which *Cyanophrys* has been parti-

tioned. To accomplish this goal, we code interspecific morphological variation to infer phylogenetic relations among *Cyanophrys* species. Besides frons color and genitalia, we code characters of the male forewing venation, androconia, brush organs (*sensu* Eliot 1973), and wing shape.

Johnson and co-authors have proposed 433 new species names in the Eumaeini during the past three decades, including 31 in *Cyanophrys* (Robbins 2004a,b), but have not been careful. The adults and genitalia of many types are different sexes or species (Robbins and Lamas 2002). Data labels on types appear to have been switched (Robbins and Nicolay 1999, Robbins and Lamas 2002). In one case, the two adult types of one species from different collections were similarly glued parts of species in different genera (Robbins and Lamas 2002). Finally, a number of types cannot be found (Robbins and Nicolay 2002, G. Lamas, personal communication).

The publications of Johnson and co-authors on *Cyanophrys* contain similar problems. For example, Johnson and Le Crom (1997b:23) designated a neotype for *Papilio amyntor* Cramer 1775 from Surinam and deposited it in the Natural History Museum (London). However, the labeled neotype deposited in this collection has data labels from French Guiana. Another specimen with their neotype label in the American Museum (New York) has a Surinam label, but is a different species than the designated neotype in London. A second representative example of their lack of care is outlined in the synopsis below under *Cyanophrys roraimiensis* K. Johnson and D. S. Smith. Although we plan to address the neotype designation elsewhere, correcting all problems created by Johnson and co-authors in *Cyanophrys* would be a Sisyphean task that could delay publication of our current results for years. We follow the classification in Robbins (2004b).

The second purpose of this paper is to present a synopsis of *Cyanophrys* species, with special emphasis on *C. bertha*. Al-

though identification of *Cyanophrys* species was not a goal of this study, the coded characters can be used to identify most species. And in the species synopsis, we note information on the distribution, habitat, identification, nomenclature, behavior, larval food plants, and published illustrations of adult *Cyanophrys* species. We summarize and assess what we know about *C. bertha* in light of the phylogenetic results.

MATERIALS AND METHODS

Genitalia, androconia, and venation were examined by standard techniques (Robbins 1991) using the approximately 1,075 specimens of *Cyanophrys* in the National Museum of Natural History (USNM) as well as others borrowed from the American Museum of Natural History (AMNH) in New York, the Illinois Natural History Survey (INHS) in Champaign–Urbana, The Natural History Museum (BMNH) in London, and the Universidade Federal do Paraná (UFPR) in Curitiba. Wing venation illustrations were made by digital scanning of wing slides. We examined 82 male and 62 female genitalic preparations. Genitalic terms follow those in Klots (1970), wing vein names follow Nicolay (1971, 1977), and androconial terminology follows Robbins (1991).

The terminal taxa are *C. goodsoni* (Clench), *C. argentinensis* (Clench), *C. bertha*, *C. acaste* (Prittwitz), *C. amyntor* (Cramer), *C. fusius* (Godman and Salvin), *C. herodotus* (Fabricius), *C. miserabilis* (Hewitson), *C. velezi* K. Johnson and Kruse, *C. crethona* (Hewitson), *C. longula* (Hewitson), *C. pseudolongula* (Clench), *C. agricolor* (Butler and H. Druce), *C. banosensis* (Clench), and *C. remus* (Hewitson). *Cyanophrys roraimiensis* K. Johnson and D.S. Smith is omitted because it is known only from the holotype female, but we discuss its likely phylogenetic placement on the basis of structures in the female type. As outgroups, we chose three species from three other subgenera of *Callophrys* recognized by Clench (1961); *Callophrys* (*Callophrys*)

Table 1. Data matrix for *Cyanophrys*. The three *Callophrys* species are the outgroups, and the characters and their states are detailed in the text.

Species	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Callophrys rubi</i>	1	0	0	0	0	0	0	0	0	0	?	?	?	?
<i>C. gryneus</i>	0	0	0	0	0	0	0	0	0	0	?	?	?	?
<i>C. niphon</i>	0	0	0	0	0	0	0	0	1	0	?	?	?	?
<i>Cyanophrys goodsoni</i>	1	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>C. argentinensis</i>	1	0	1	0	1	0	1	1	0	0	0	0	0	0
<i>C. bertha</i>	0	0	0	0	1	0	1	1	2	0	0	1	0	0
<i>C. acaste</i>	1	0	1	1	1	0	1	1	2	0	0	1	0	0
<i>C. amyntor</i>	1	0	0	1	1	0	1	1	2	0	0	1	0	0
<i>C. fusius</i>	1	1	0	2	?	?	1	1	2	0	0	1	0	0
<i>C. herodotus</i>	1	1	0	1	1	1	1	1	2	1	0	0	0	0
<i>C. miserabilis</i>	0	1	0	1	1	1	1	1	2	1	0	0	0	0
<i>C. velezi</i>	0	1	0	1	1	1	1	1	2	1	0	0	0	0
<i>C. crethona</i>	0	1	0	1	1	1	1	1	2	1	0	0	0	0
<i>C. longula</i>	0	0	0	0	1	0	1	1	2	0	1	0	1	1
<i>C. pseudolongula</i>	0	?	0	0	1	0	1	1	2	0	1	0	1	1
<i>C. remus</i>	0	1	0	0	1	0	1	1	2	0	1	0	1	1
<i>C. banosensis</i>	0	1	0	0	1	0	1	1	2	0	1	0	1	1
<i>C. agricolor</i>	0	1	0	0	1	0	1	1	1	0	1	0	1	1

rubi (L.), *C. (Mitoura) gryneus* (Hübner), and *C. (Incisalia) niphon* (Hübner).

We coded 14 characters (Table 1) and used a question mark (?) for inapplicable states and for one case of an intraspecific dimorphism. All multi-state characters were treated non-additively (unordered). We used the implicit enumeration option of Hennig86 software to derive most parsimonious cladograms. A strict consensus tree was determined. To test the assumption of equally weighted characters, a successive weighting iteration was performed (Farris 1969), and a consensus of the resulting trees was determined. Mapping of characters on trees was done with Winclada software (Nixon 2002) using the "unambiguous changes only" optimization option. Jackknife supports were determined in Winclada using Nona (1000 replications with mult*10, memory 1000 trees).

The synopsis contains additional detail for *C. bertha* because of its conservation interest. The distribution of *C. bertha* is based on 13 museum specimens (Appendix). Its morphology is based on 6 individuals in the USNM collection (Appendix).

Distributional information for the other species is based on specimens from many museums and from the literature. Records of larval food plants without citation are based on Janzen and Hallwachs (2004) or data compiled by Robbins. Plant family names follow those in Willis (1973). Records of "territorial" behavior are based on unpublished data compiled by Robbins. Type localities are listed in Robbins (2004b), and citations for original descriptions can be found in Lamas (1995).

MORPHOLOGY AND CODED CHARACTERS

Head.—Presence or absence of iridescent green scales on the frons is intraspecifically consistent.

Character 1: Iridescent green scales on frons (0) absent, (1) present.

This character needs to be used with caution because exposure to humidity, particularly during preparation, or to physical abrasion can change scale color from green to brown. Iridescent butterfly scales return to their original color after drying (Nijhout 1991), but for reasons currently unknown, this is generally untrue for hairstreaks

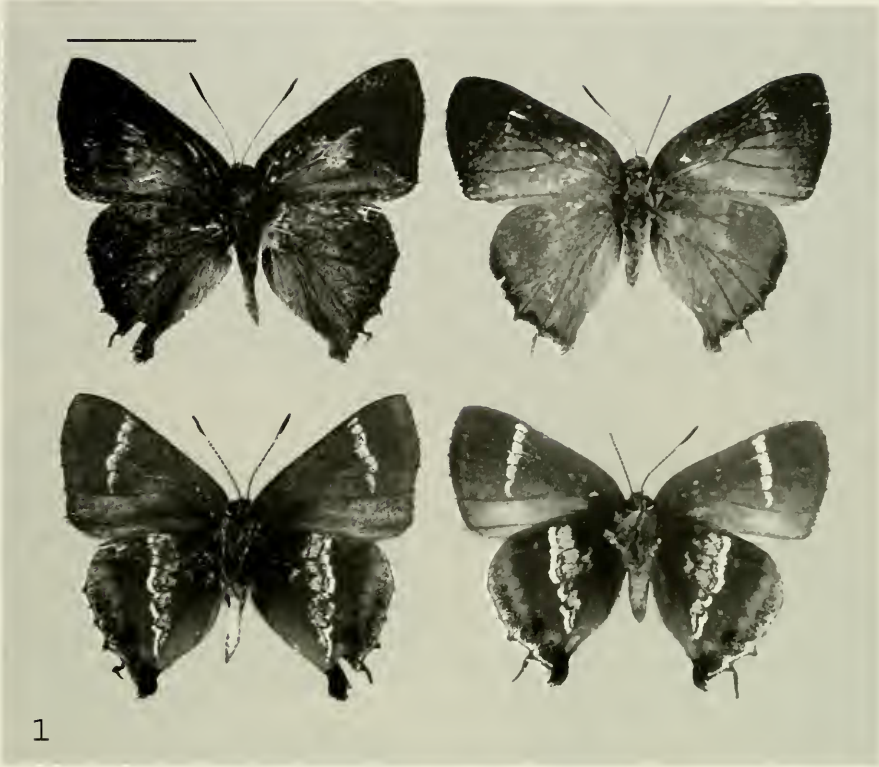


Fig. 1. Dorsal (top) and ventral wings of male (left) and female *Cyanophrys berthia*. Scale 1 cm.

(Robbins, unpublished). Also, green scales on the frons may be rubbed off of worn individuals.

Wing pattern.—We were unable to code wing pattern variation in *Cyanophrys* for a number of reasons. Presence of a postmedian line on the ventral forewing varies interspecifically and intraspecifically among species. A dark maroon band along the submargin of the ventral hindwing and dark brown scales at the base of the ventral hindwing are conspicuous wing pattern elements in some *Cyanophrys* species, but the dark maroon and brown scales occur in all *Cyanophrys* and the extent of their expression shows almost continuous variation among species and sometimes within a species.

Male wing venation.—Male forewing venation varies within *Cyanophrys*, and we code it as two characters.

Character 2: Male forewing veins R3

and M1 (0) connected by vein UDC, which may be poorly developed (Figs. 3, 5–7), (1) fused at the origin of vein M1 (vein UDC absent) (Fig. 4). Males of *C. pseudolongula* are coded with a question mark because they are geographically variable for forewing venation, with both states occurring in males from Ecuador and northern Peru east of the Andes.

Character 3: Male forewing veins R2 and R3 (0) arise from the discal cell (Figs. 3–4, 6), (1) are stalked (Fig. 5).

Androconia.—There are three major androconial patterns. Males of some *Cyanophrys* species have two clusters of androconia; one at the base of veins R2, R3, and M1 and one along the base of vein M3 (Figs. 4–5). Other species have androconia only at the base of veins R2, R3, and M1 (Figs. 3, 6–7), although this cluster is sometimes small, as in *C. remus*. Finally, males of *C. fusius* are unique among *Cyanophrys*

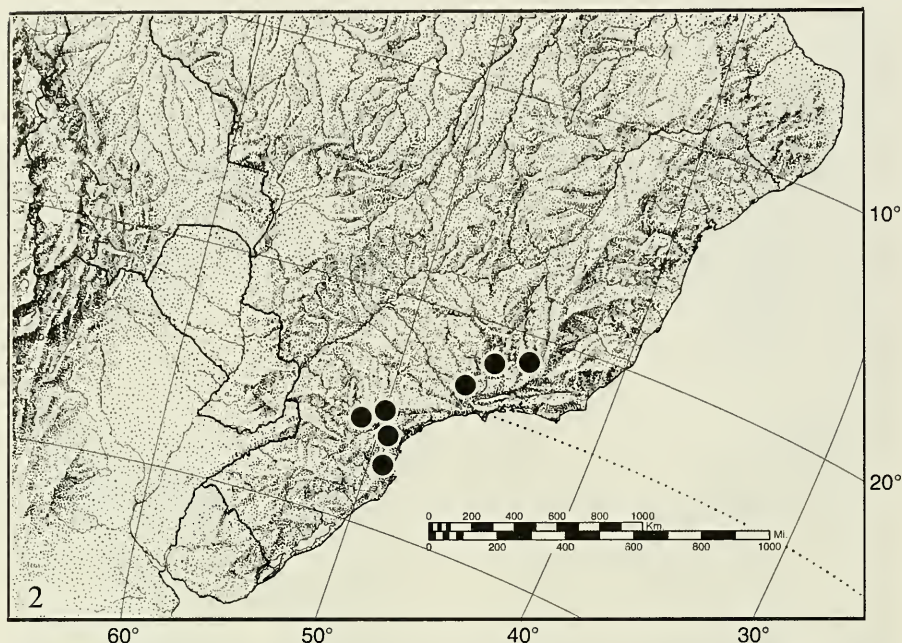


Fig. 2. Distribution of *Cyanophrys berthia* in southern Brazil from 13 museum specimens (Appendix).

in having brown dorsal forewings (iridescent blue in the others) that lack androconia. Because it lacks androconia, *C. fusius* was coded ? (inapplicable) for characters 5–6.

Character 4: Male dorsal forewing (0) with androconia only at the base of veins R2, R3, and M1 (Figs. 3, 6–7), (1) with androconia at the base of veins R2, R3, and M1 and along the base of vein M3 (Figs. 4–5), (2) lacking androconia.

Character 5: Dorsal forewing androconial cluster at the base of veins R2, R3, and M1 (0) extends into cell R2-R3 (Figs. 6–7), (1) absent from cell R2-R3 (Fig. 3–5).

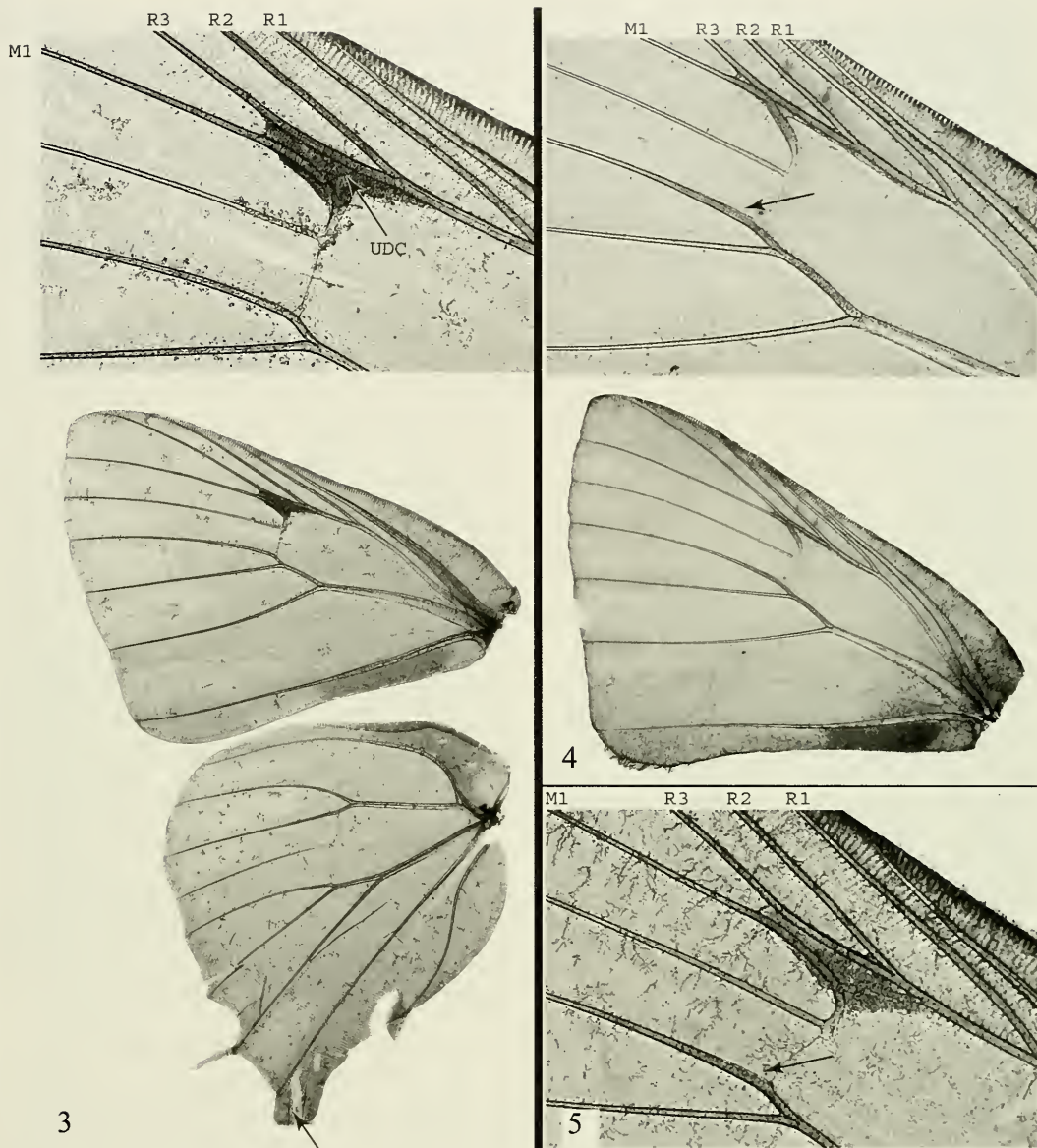
Character 6: Basal edge of dorsal forewing androconial cluster at the base of veins R2, R3, and M1 (0) located at, or just basal to, the origin of vein R2 (Figs. 3, 5–7), (1) extending basally well beyond the origin of vein R2 to, or almost to, the origin of vein R1 (Fig. 4).

Wing shape and hindwing tails.—Despite variability in wing shape and number of hindwing tails, we code only one such character. We did not code number of tails be-

cause it can vary between males and females (*C. longula*), geographically (*C. herodotus*, *C. acaste*), or at one locality (*C. amyntor*, *C. herodotus*). We also did not code wing shape because there appears to be a continuum of variation from the rounded wings of *C. goodsoni* to the angular wings of *C. agricolor*. The character below, however, is distinct and unambiguously scored.

Character 7: Hindwing anal lobe (0) not produced posteriorly (<0.1 mm beyond the outer margin of cell Cu2–2A) (Fig. 7), (1) produced posteriorly, at least 0.25 mm beyond the outer margin of cell Cu2–2A (Figs. 3, 6).

Male genitalia.—We found considerable interspecific variation in the male genitalia and its associated dorsal brush organs. Variation of some structures, such as length of the saccus (Table 2), phallobase (internal part of the penis), entire penis, and tegumen, was not phylogenetically useful because differences in means between species were small (typically less than one standard deviation), which made it difficult to rec-



Figs. 3–5. Forewing and hindwing venation with detail of androconial clusters. 3, *Cyanophrys berthia*. Arrow at top points to the upper discocellular vein (UDC), which arises distal of the origin of vein R2. Arrow at bottom points to the posteriorly produced hindwing anal lobe. 4, *C. herodotus*. Detail shows anastomosis of veins R3 and M1; there is no upper discocellular vein. Arrow points to androconia along the base of vein M3. 5, *C. acaste*. Veins R2 and R3 are stalked. Arrow points to androconia along the base of vein M3. The upper discocellular vein arises basal of the origin of vein R2.

ognize distinct states. We were able to code other aspects of interspecific variation. Because they lack brush organs, the outgroup species were coded? (inapplicable) for characters 11–14.

Character 8: Dorsal male genitalia brush organs (0) absent, (1) present (Figs. 8–10).

Character 9: Male genitalia valvae (0) with a terminal thickening that extends along the inner margin of the valva (Fig. 3

Table 2. Mean length in mm of the saccus measured in ventral aspect along the sagittal plane. Species are listed in ascending rank order with differences between succeeding species typically less than a standard deviation.

Species	Mean Length	Standard Deviation	Sample Size
<i>C. acaste</i>	0.53	0.050	7
<i>C. remus</i>	0.54	0.036	5
<i>C. amyntor</i>	0.61	0.086	5
<i>C. agricolor</i>	0.64	0.042	4
<i>C. pseudolongula</i>	0.68	0.036	3
<i>C. longula</i>	0.69	0.035	4
<i>C. berthia</i>	0.72	0	2
<i>C. herodotus</i>	0.74	0.062	7
<i>C. velezi</i>	0.79	0.051	2
<i>C. goodsoni</i>	0.79	0.204	2
<i>C. fusius</i>	0.81	0.091	4
<i>C. argentinensis</i>	0.82	0.062	4
<i>C. banosensis</i>	0.83	0	1
<i>C. miserabilis</i>	0.86	0.030	5
<i>C. crethona</i>	1.35	0.040	2

in Warren and Robbins 1993), (1) with a strongly demarcated terminal thickening that does not extend along the inner margin of the valva (Fig. 10, Fig. 3 in Warren and Robbins 1993), (2) with no terminal thickening ("not capped" in Clench 1961) (Figs. 8–9).

Clench (1961) reported valva tips with a terminal thickening in subgenera *Incisalia*, *Sandia* Clench and Ehrlich, and *Xamia* Clench. This valva tip was illustrated by Warren and Robbins (1993), and also occurs in *C. agricolor*. A less prominent thickening that extends along the inner margin of the valvae occurs in subgenera *Callophrys* and *Mitoura* (Warren and Robbins 1993) as well as *C. goodsoni* and *C. argentinensis*.

Character 10: Posterior-ventral process of vinculum-tegumen (0) less than 0.15 mm in length (Figs. 8, 10), (1) with a long (> 0.15 mm) pointed process (Fig. 9).

Character 11: Anterior end of the setae comprising the dorsal male genitalia brush organs oriented (0) dorso-posteriorly (Figs. 8, 9), (1) horizontally (Fig. 10).

Character 12: Distance from anterior to

posterior ends of the dorsal male genitalia brush organs in lateral aspect (0) less than 1.3 mm long (Figs. 9–10), (1) more than 1.4 mm long (Fig. 8).

Character 13: Anterior end of the dorsal male genitalia brush organs originates in lateral aspect (0) near or below the origin of the vinculum strut (Figs. 8–9), (1) primarily above the origin of the vinculum strut (Fig. 10).

Character 14: Width of the dorsal male genitalia brush organs (dorsal aspect) at its widest point (0) less than 0.5 mm (Figs. 8–9), (1) more than 0.5 mm (Fig. 10).

Female genitalia.—Although length and width of the ductus bursae, development of sclerotized plates surrounding the ostium bursae, and length of the spines of the signa vary in *Cyanophrys*, we did not code this variation. For the ductus bursae, mean lengths and widths for species were similar, which made it difficult to delineate distinct states. Similarly, we were unable to characterize distinct states among species in development of the lamellae vaginalis or spines of the signa. In brief, interspecific variation in the female genitalia was not phylogenetically informative even though it was sometimes useful for distinguishing species, such as *C. herodotus* and *C. amyntor*. The bursa copulatrix of *C. berthia* is illustrated (Fig. 11).

PHYLOGENETIC ANALYSES AND RESULTS

Analysis of the character matrix with the Hennig86 "ie*" option, which searches exhaustively for the most parsimonious cladograms, yielded 15 equally parsimonious 23-step trees with a consistency index of 0.69 and retention index of 0.86. The equally parsimonious trees differed primarily in the placement of *C. berthia* and *C. fusius*, with *C. berthia* being the sister of either the *C. longula* group (*C. longula*, *C. pseudolongula*, *C. agricolor*, *C. banosensis*, and *C. remus*) or *C. herodotus* group (*C. acaste*, *C. amyntor*, *C. fusius*, *C. herodotus*, *C. miserabilis*, *C. velezi*, and *C. crethona*). This result is represented in the consensus tree

("nelsen" option) as a trichotomy among *C. bertha*, the *C. longula* group, and the *C. herodotus* group, but the latter group is not strongly supported (Fig. 12 with jackknife values). The consensus tree is not one of the 15 most parsimonious trees.

A successive weighting iteration (Farris 1969) produced three trees, each of which was one of the 15 original most parsimonious ones. Wing venation and frons color (characters 1–3) were weighted four or less out of 10 while the other characters (4–14) were fully weighted (10 out of 10) except for "capped" valvae (character 9) and brush organ length (character 12). In other words, androconia and male genitalia characters were less likely to be homoplastic than those of wing venation and frons color. Carpenter (1988) argued that these trees are the best phylogenetic hypotheses. The consensus of the three successively weighted trees (24 steps) shows a sister relationship between *C. bertha* and the *C. herodotus* lineage, and there is greater resolution within the *C. herodotus* group (Fig. 13) than in the original consensus tree (Fig. 12).

MONOPHYLY OF GENERA AND SUBGENERA

Hypothesized synapomorphies for *Cyanophrys* are (1) paired dorsal brush organs on the intersegmental membrane between the male genitalia vinculum and the 8th abdominal tergum (Character 8, Figs. 8–10) and (2) an elongate hindwing anal lobe with tan-brown coloration (Character 7, Figs. 3, 6). These synapomorphies are unique in the *Callophrys* Section (Robbins 2004b), but occur in other sections of the Eumaeini. However, the green underside of the wings coupled with the elongate hindwing anal lobe allow adult *Cyanophrys* to be identified in the field. These results do not provide data on whether the Holarctic members of *Callophrys* (*sensu* Clench 1961) form a monophyletic group.

Cyanophrys as characterized in this paper has been partitioned into subgenera (sometimes treated as genera) *Cyanophrys*, *Plesiocyanophrys* K. Johnson, Eisele and

MacPherson, *Antephrys* K. Johnson, Eisele and MacPherson, *Apophrys* K. Johnson and Le Crom, and *Mesocyanophrys* K. Johnson (Johnson et al. 1993, Johnson and Le Crom 1997a). The species that belong to each is noted (Fig. 12). Subgenus *Cyanophrys* contains the *C. longula* group (as denoted above), *C. miserabilis*, *C. velezi*, *C. crethona*, and *C. roraimiensis* (the latter omitted from the phylogenetic analysis) (Johnson and Le Crom 1997a). This grouping is polyphyletic in the 15 original most parsimonious cladograms, as summarized by the consensus tree (Fig. 12). Subgenus *Plesiocyanophrys* contains *C. goodsoni* and *C. argentinensis* (Johnson et al. 1993), a grouping that is paraphyletic in the 15 most parsimonious trees. Subgenus *Antephrys* contains only *C. fusius* (Johnson et al. 1993, Johnson and Le Crom 1997a, Johnson and Amarillo 1997, Robbins 2004b), making it a monotypic genus. Subgenus *Mesocyanophrys* contains *C. acaste* and *C. bertha* (Johnson and Le Crom 1997a), a grouping that is paraphyletic or polyphyletic in the original 15 most parsimonious trees. Finally, subgenus *Apophrys* contains *C. herodotus* and *C. amyntor* (Johnson and Le Crom 1997a), a grouping that is not monophyletic in the 15 most parsimonious cladograms.

SYNOPSIS OF SPECIES

Cyanophrys goodsoni (Clench, 1946)

Distribution, habitat, and abundance.—Usually uncommon in seasonally dry habitats from southern Texas (United States) to Guanacaste (Costa Rica).

Larval food plants.—Blossom buds of *Rivina* (Phytolaccaceae) in Texas and on *Vernonia* (Compositae) in Costa Rica.

Illustrations of adults.—Both sexes in Scott (1986).

Cyanophrys argentinensis (Clench, 1946)

Distribution, habitat, and abundance.—Uncommon to rare in both dry and wet forests from sea level to over 1,000 m elevation from eastern Panama (Darien) and



Figs. 6-7. Forewing and hindwing venation with detail of androconial clusters. 6, *Cyanophrys goodsoni*. Arrow at top points to the upper discocellular vein. Arrow at bottom points to the posteriorly produced hindwing anal lobe. 7, *Callophrys rubi*. Arrow at top points to the upper discocellular vein. Arrow at bottom points to the hindwing anal lobe that is not posteriorly produced.

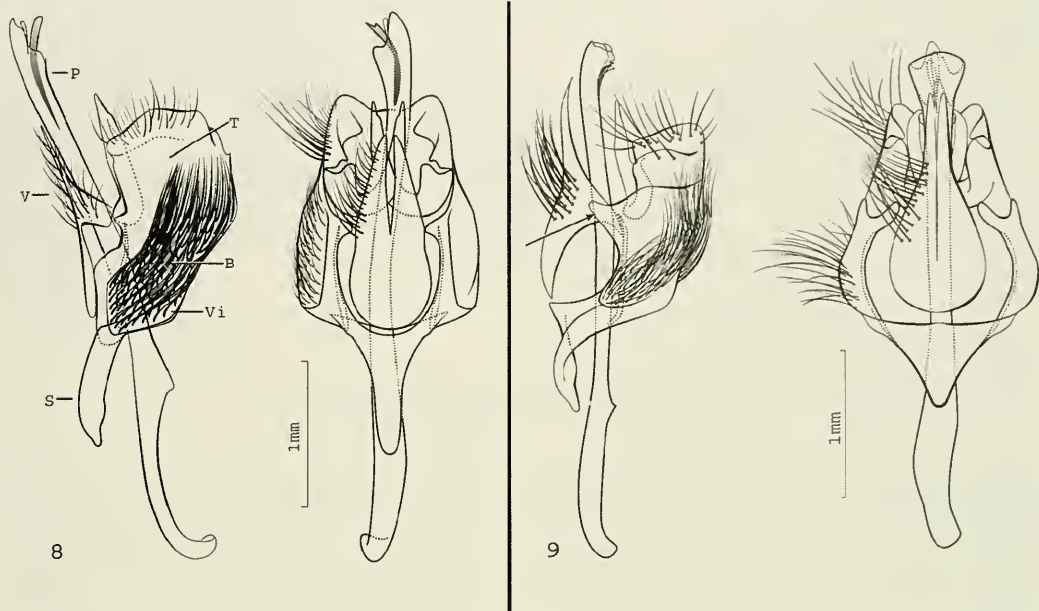
northern Venezuela (Aragua) south along the Andes to northwestern Argentina, then eastward to Paraguay and southern Brazil.

Variation—Width of the ductus bursae in the middle in ventral aspect appears to vary geographically, from more than 0.30 mm

(Panama, Venezuela) to 0.25 mm (Peru) to 0.20 mm (Argentina).

Male behavior.—A "territorial" male was recorded at about 1400 hours on a hilltop.

Illustrations of adults.—Both sexes in D'Abrera (1995).



Figs. 8–9. Male genitalia in lateral (left) and ventral aspect. 8, *Cyanophrys berthae*. B-brush organs, P-penis, S-saccus, T-tegumen, V-valvae, Vi-vinculum (which is fused with the tegumen in all eumacines). 9, *C. herodotus*. The arrow points to the ventro-lateral process of the tegumen, which is foreshortened in this aspect.

Cyanophrys berthae (Jones, 1912)

Distribution.—Coastal mountains of southern Brazil from about 800 to 1,400 m elevation in the states of Minas Gerais, São Paulo, Paraná, and Santa Catarina (Fig. 2, Appendix). There are literature records from Rio de Janeiro (Brown 1993) and Rio Grande do Sul (Draudt 1919–1920), but we know of no extant specimens to verify the occurrence of *C. berthae* in these states. The elevation of the locality where one specimen was supposedly collected is 75 m, but it is probably mislabeled (discussed in Appendix).

Habitat.—The habitat of *C. berthae* is varied. Holdridge's (1947) ecological life zones of the localities in the Appendix include subtropical lower montane moist forest, subtropical moist forest, and warm temperate moist forest (Tosi 1983). Vegetation zones include dense evergreen forest, mixed evergreen forest, and seasonally deciduous forest (IBGE 1993). Although *C. berthae* appears to be primarily a resident of

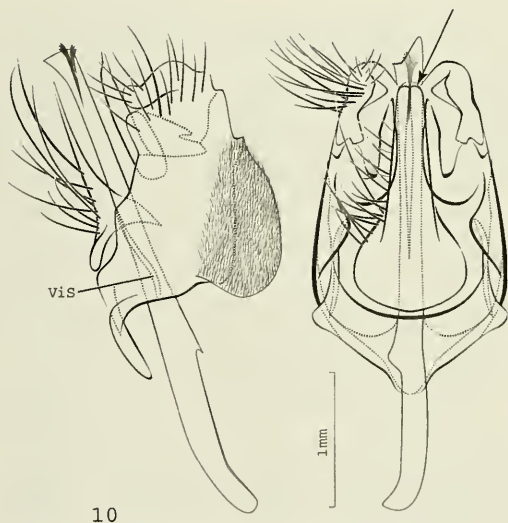
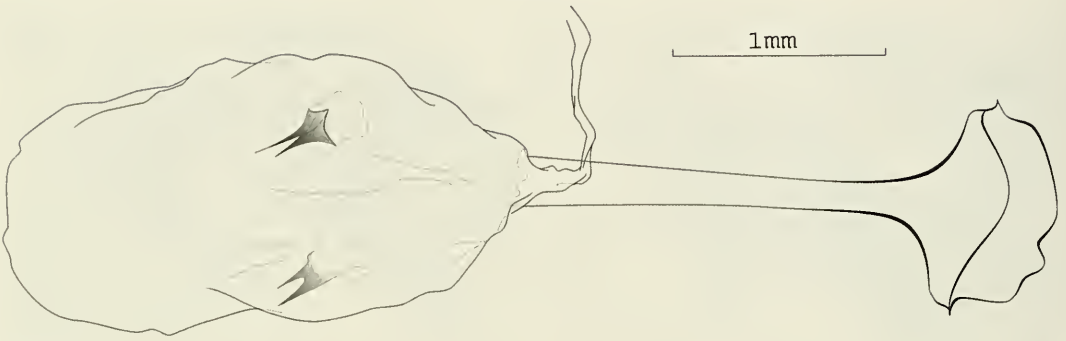


Fig. 10. Male genitalia of *Cyanophrys agricolor* in lateral (left) and ventral aspect. The arrow (right figure) points to terminal thickening of valvae. ViS—vinculum strut, which is an internal ridge.



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Fig. 11. Female genitalia bursa copulatrix of *Cyanophrys berthia* in ventral aspect.

moist coastal mountains, three specimens found at Barbacena (Minas Gerais) indicate that it also occurs, at least on occasion, in semi-deciduous forest and may possibly be more widespread inland than is currently realized.

Identification.—The unique ventral wing pattern of *C. berthia* (Fig. 1) has distinguished this species since it was described.

Larval food plants.—The larval food plant and immature stages of *C. berthia* are unknown. Larvae of other *Cyanophrys* have been reared on flowers, fruits, or young leaves of plants in families Anacardiaceae, Boraginaceae, Dipsacaceae, Compositae, Leguminosae, Malvaceae, Phytolaccaceae, Sambucaceae, Sterculiaceae, Ulmaceae, and Verbenaceae.

Male behavior.—Brown (1993) observed males of *C. berthia* setting up mating territories in the crowns of trees on hilltops at Serra do Japi (cf. Appendix) in the early afternoon. Other than *C. velezi*, whose males set up mating territories on hilltops before 0930 hours, the afternoon male “territorial” behavior of *C. berthia* is typical for the genus.

Illustrations of adults.—Fig. 1.

Cyanophrys acaste (Prittwitz, 1865)

Distribution, habitat, and abundance.—A very common species in a variety of habitats and elevations from southern Brazil to eastern Bolivia, south to central Argentina and Uruguay.

Variation.—Variation of the ventral wing pattern, particularly expression of the post-median line and a white hindwing discal bar, accounts for this species being named repeatedly, usually as a subspecies. Individuals from the southern temperate parts of the range are tailed (*C. acastoides* phenotype).

Larval food plants.—*Chuquiraga* (Compositae) in Brazil.

Male behavior.—Males “perch” on hilltops from about 1100 to 1500 hours.

Illustrations of adults.—Both sexes in D’Abrera (1995).

Cyanophrys amyntor (Cramer, 1775)

Distribution, habitat, and abundance.—Widespread and common from sea level to about 1,100 m from northern Mexico to southern Brazil. Recorded from Texas, United States (Kendall and McGuire 1984), based on a female in the Illinois Natural History Survey. Johnson and Le Crom (1997b) stated that it was a misidentified female of *C. herodotus*. Robbins (unpubl.) confirmed their identification.

Variation.—Individuals in the southern parts of its range may have or lack tails, but do not differ otherwise. The name *Cyanophrys caramba* (Clench) refers to tailless individuals.

Identification.—Slightly larger on average than sympatric *C. herodotus*, but males are distinguished by different androconial

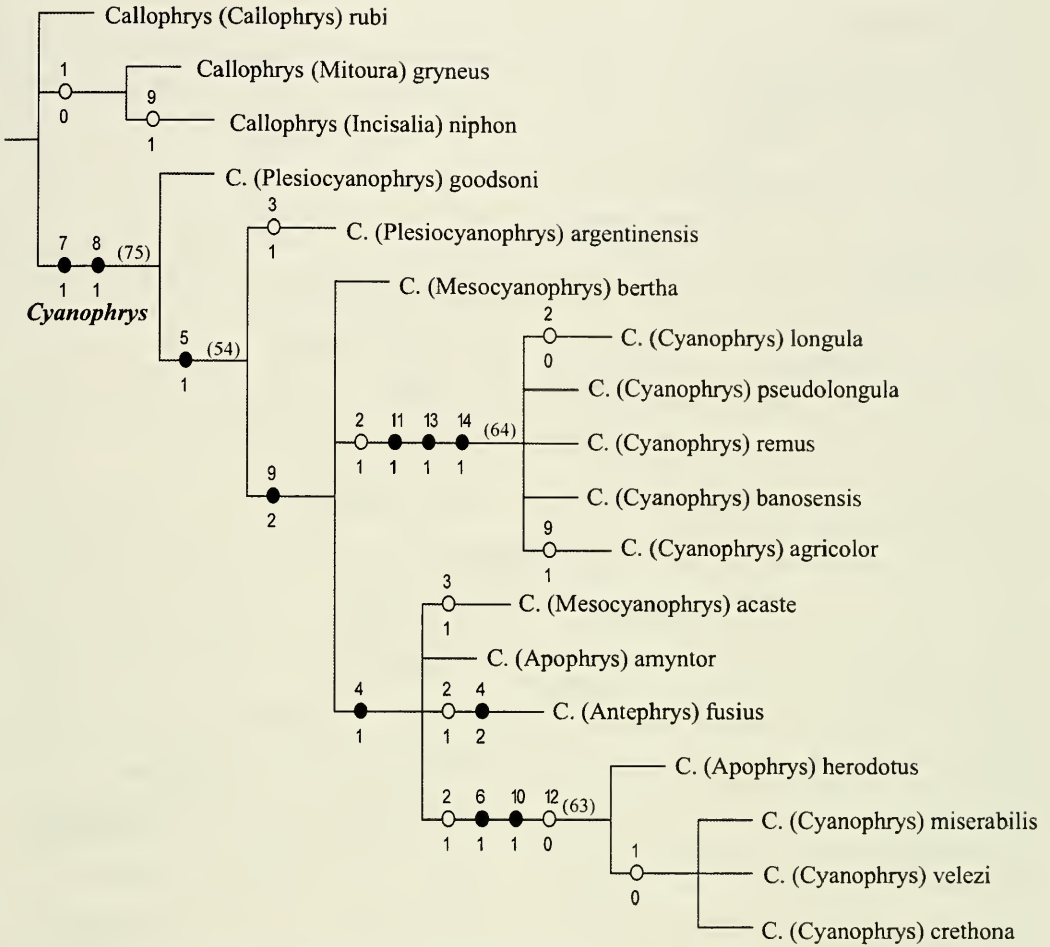


Fig. 12. Strict consensus of the fifteen equally most parsimonious cladograms (23 steps, $ci = 0.69$, $ri = 0.86$) for *Cyanophrys* species. *Callophrys rubi*, *C. gryneus*, and *C. niphon* (top) are outgroups. Character numbers are placed above nodes and character state numbers below nodes. Open circles represent reversal or convergence of the character state at that node. Jackknife values are noted in parentheses. Subgeneric placements for *Cyanophrys* from Johnson et al. (1993), Johnson and Le Crom (1997a), and Johnson and Amarillo (1997)

patches on the dorsal forewing. Females of the two have different genitalia.

Larval food plants.—Reared from Ulmaceae (*Celtis*, *Trema*) in Mexico, Ecuador, and Brazil (Kendall 1975, Hoffmann 1937), and from Verbenaceae (*Clerodendron*) in Trinidad.

Male behavior.—Males set up mating territories along trail edges and on hilltops from about 1200 to 1600 hours.

Illustrations of adults.—Male in D'Abbrera (1995), but identity of the female that he illustrated as this species is unclear.

Cyanophrys fusius
(Godman and Salvin, 1887)

Distribution, habitat, and abundance.—Seasonally dry habitats from northern Mexico to Colombia and Venezuela (Clench 1946).

Identification.—Males are brown above, not blue, and lack forewing androconia, both unique traits in *Cyanophrys*. Clench (1946) noted the similarity of females of this and the previous species, but female *C. fusius* have a short white-tipped tail at the end of vein Cu_1 while Central American

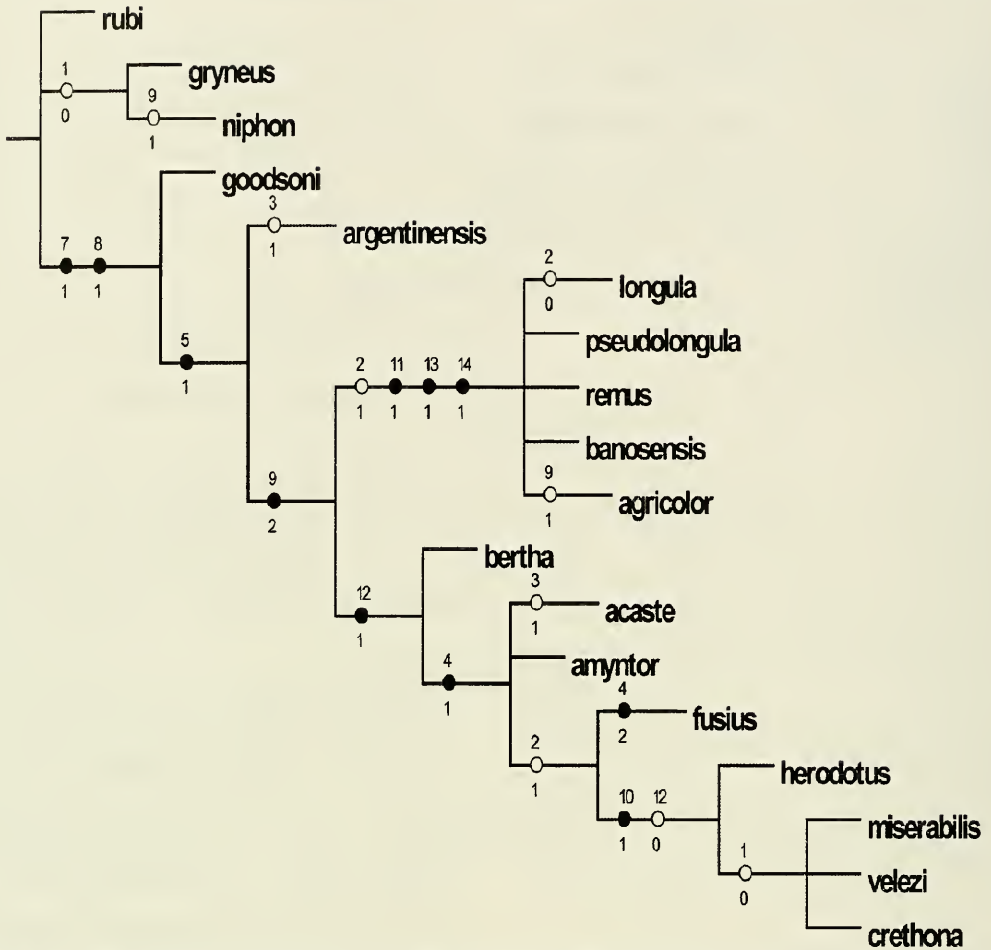


Fig. 13. Strict consensus of the three most parsimonious successively weighted trees for *Cyanophrys* species. Characters of wing venation and frons color were under-weighted because they were homoplastic.

females of *C. amyntor* have only a black stub at the end of vein Cu1.

Larval food plants.—Reared from *Arrabidaea* (Bignoniaceae) in Costa Rica.

Male behavior.—A “territorial” male was collected on a ridge top at 1500 hours.

Illustrations of adults.—Male in D’Abrera (1995), but identity of the female that he illustrated as this species is unclear.

Cyanophrys herodotus (Fabricius, 1793)

Distribution, habitat, and abundance.—The most common, widespread, variable, and weedy species in *Cyanophrys*, occurring in almost all habitats under 1,500 m throughout the Neotropics.

Variation.—Size and wing pattern of this species are highly variable, with the largest individuals being most frequent in the southern part of the range. Individuals from northwestern Peru, western Ecuador and Colombia, and northern Colombia lack a tail (to which the name *C. detesta* refers), but do not otherwise differ. Specimens with and without a tail occur sympatrically and synchronically in El Salvador and southern Brazil, but again, do not otherwise differ. Despite substantive genitalic variation, including clinal differences, we find no convincing evidence of sibling species.

Larval food plants.—A polyphagous species that has been reared from plants in the

Anacardiaceae, Boraginaceae, Compositae, Dipsacaceae, Malvaceae, Sambucaceae, and Verbenaceae (Lima 1928, 1930, 1936; Santos 1933; Monte 1934; Biezanko et al. 1974; Robbins and Aiello 1982).

Male behavior.—Males set up mating territories on hilltops and ridges in the middle of the afternoon from about 1300 to 1600 hours at slightly greater heights above the ground, on average, than males of *C. amyntor*.

Illustrations of adults.—Male in D'Abrera (1995), but identity of the female that he illustrated as this species is unclear.

Cyanophrys miserabilis (Clench, 1946)

Distribution, habitat, and abundance.—Occurs in seasonally dry habitats from sea level to about 2,000 m elevation from southern United States (Texas) to the Pacific side of Costa Rica.

Identification.—It is easily distinguished from the sympatric *C. herodotus* by the brown frons (green in *C. herodotus*) and by the greater amount of dark maroon scaling along the outer margin of the ventral hindwing. *Cyanophrys miserabilis* appears to form a superspecies (monophyletic lineage in which no two species are sympatric) with the next two species (Figs. 12, 13). Besides the presumed evolution of a brown frons in the ancestor of these species, they also possess "thin, stringy" brush organs.

Larval food plants.—Recorded larval food plants are Compositae (*Eupatorium*) and Leguminosae (*Caesalpinia*, *Parkinsonia*).

Illustrations of adults.—Both sexes in D'Abrera (1995).

Cyanophrys velezi

Johnson and Kruse 1997

Distribution, habitat, and abundance.—Occurs in Panama, where it has been recorded only during the dry season, to western Ecuador in seasonally dry habitats.

Identification.—Unlike *C. miserabilis*, it lacks a hindwing tail and dark maroon scal-

ing along the outer margin of the ventral hindwing.

Male behavior.—Males "hilltop" in the morning before 0930 hours, which is unique in the genus, so far as is known, but which may be shared by the preceding and succeeding species.

Illustrations of adults.—This species has been illustrated, so far as we are aware, only in the original description.

Cyanophrys crethona (Hewitson, 1874)

Distribution, habitat, and abundance.—A Jamaican endemic.

Identification.—The male genitalia of *C. crethona* is similar to the preceding two species, but is distinguished by its larger size (i.e., Table 2) and a very lightly sclerotized ventral cornutus.

Nomenclature.—*Cyanophrys hartii* Turner and J. Y. Miller differs from *C. crethona* by ventral brown coloration. Because exposure to humidity or physical abrasion can change scale color from green to brown, as mentioned in the discussion of Character 1, this name was synonymized with *C. crethona* (Robbins 2004b).

Illustrations of adults.—A male is illustrated in D'Abrera (1995).

Cyanophrys roraimiensis Johnson and Smith, 1993

Distribution, habitat, and abundance.—Known only from the holotype female, which was collected on the Brazilian side of Mt. Roraima. We have seen a picture of a female collected in the adjoining tepui region of Venezuela that may be this species, but have not had the opportunity to examine it.

Identification.—The ventral hindwing pattern and size of this species is exceedingly similar to that of *C. crethona* (Huntington 1933, Comstock and Huntington 1943), with which it also shares a brown frons, for which reason we suspect that it is closely related to the preceding three species.

Nomenclature.—Johnson and Smith

(1993) wrote that Comstock and Huntington (1943) mentioned other specimens of *Cyanophrys roraimiensis*. Johnson and Smith (1993) then noted that these specimens were missing and speculated at length on the reasons why they had been "stolen." However, neither Huntington (1933) nor Comstock and Huntington (1943) mentioned any specimens of this species other than the one that was subsequently designated the holotype.

Illustrations of adults.—This species has not been illustrated other than in the original description.

Cyanophrys longula (Hewitson, 1868)

Distribution, habitat, and abundance.—A common species that occurs above 800 m from northern Mexico to western Panama. This species has been recorded as a stray in Arizona, United States (Bailowitz and Brock 1991), but no voucher specimen or photograph exists, so far as we are aware.

Identification.—Males are tailless and females have a single tail. This and the following 4 species appear to form a monophyletic lineage of montane species that is uniquely characterized by brush organ structure, as described in the text (Fig. 10).

Larval food plants.—Larvae have been reared from Compositae (*Eupatorium*) and Verbenaceae (*Lantana*, *Stachytarpheta*).

Male behavior.—"Territorial" males have been recorded during the late morning (1000–1130 hours) on trees at the edge of a road, but the hours of such activity may depend largely upon good weather.

Illustrations of adults.—Both sexes in D'Abrera (1995).

Cyanophrys pseudolongula (Clench, 1944)

Distribution, habitat, and abundance.—A common species above 700 m elevation in the Andes from Venezuela to Argentina and east through Paraguay to the mountains of southern Brazil. In the southern subtropical parts of its range, it may occur at lower elevations.

Variation.—Males in the northern part of

the range (Venezuela and Colombia to western Ecuador and Peru) have relatively small androconial clusters and forewing veins R3 and M1 fused in contrast to those from the south (central Peru to southern Brazil, for which the name *C. longuloides* Clench was proposed) with larger androconial clusters and forewing veins R3 and M1 connected by vein UDC. However, some males in Ecuador and northern Peru east of the Andes have intermediate venation (veins R3 and M1 "touch," a small vein UDC) as well as intermediate sized androconial clusters (although closer to the northern phenotype).

Larval food plants.—*Calliandra* (Leguminosae), *Abutilon* (Malvaceae), *Pavonia* (Malvaceae), and *Buettneria* (Sterculiaceae) (Biezanko et al. 1974).

Male behavior.—"Hilltopping" males have been recorded from 1340 to 1415 hours.

Illustrations of adults.—Both sexes in D'Abrera (1995).

Cyanophrys agricolor
(Butler and Druce, 1872)

Distribution, habitat, and abundance.—Occurs commonly in the mountains of Central America above 1,000 m elevation.

Variation.—A short series of males collected at 1,400 m on the wet Atlantic side of Panama (Veraguas) are considerably brighter blue above, but do not differ in any other way.

Male behavior.—Males have been observed setting up mating territories on trees lining a dirt road from 1000 to 1430 hours.

Illustrations of adults.—Both sexes in D'Abrera (1995).

Cyanophrys banosensis (Clench, 1944)

Distribution, habitat, and abundance.—A montane species that usually occurs above 1500 m from Venezuela to southern Peru. Although rare to uncommon in museum collections, it has recently been found commonly in both wet and dry montane habitats in Ecuador (Busby and Hall, pers. comm.).

It probably occurs in Bolivia, but we know of no records.

Illustrations of adults.—A female is illustrated in D'Abrera (1995).

Cyanophrys remus (Hewitson, 1868)

Distribution, habitat, and abundance.—A very common species in the mountains of southern Brazil, Argentina (Misiones), Uruguay, and Paraguay. In the subtropical parts of its range, it occurs at lower elevations.

Identification.—Males have brilliant dorsal blue color, similar to that in *C. longula* and *C. pseudolongula*, but the underside wing pattern has extensive brown markings, similar to the preceding two species.

Larval food plants.—It has been reared from *Calliandra* (Leguminosae) in Uruguay and from *Abutilon* and *Pavonia* (Malvaceae) in Brazil (Zikán 1956, Biezanko et al. 1966, Silva et al. 1968).

Male behavior.—Males "hilltop" in the early afternoon, with records from 1145 to 1500 hours.

Illustrations of adults.—Both sexes in D'Abrera (1995).

DISCUSSION

Building on the work of Clench (1961), Robbins (2004a) distinguished the *Callophrys* Section of the Eumaeini by valve tips that are flattened and without setae, but sometimes with a terminal thickening (illustrated in Warren and Robbins 1993). The form of the anal lobe (Character 7) and presence of brush organs (Character 8) distinguish *Cyanophrys* from other members of the *Callophrys* Section. Although the genus could be split into smaller genera on the basis of the phylogenetic results (Figs. 12 and 13), the anal lobe character allows individuals to be recognized in the field. It is unclear whether the remaining Holarctic members of *Callophrys*, or the many genera into which they have been divided, are monophyletic.

The subgeneric nomenclature used by Johnson and colleagues (Johnson et al. 1993, Johnson and Le Crom 1997a, John-

son and Amarillo 1997) is inconsistent with the phylogenetic results (Fig. 12). Four of these subgenera are not monophyletic and one is monotypic. In some cases, such as the aptly named *Plesiocyanophrys*, they appear to have been characterized with symplesiomorphies. In others, such as the characterization of *Cyanophrys* (a brown frons), they were delimited by a homoplastic character.

The *C. longula* and *C. herodotus* groups are monophyletic on the 15 most parsimonious trees. The *C. longula* group consists of species with a brown frons (Character 1, which is homoplastic), brush organs wider than 0.05 mm (Character 14, Fig. 10), brush organs that are oriented horizontally at the anterior end (Character 11, Fig. 10), and brush organs that arise primarily above the origin of the vinculum strut (Character 13, Fig. 10). The latter three character states are unique in the *Callophrys* Section. These species occur in montane habitats (above 800 m) except in the subtropical parts of southern South America. The *C. herodotus* group consists of species with two androconial clusters on the dorsal forewing (Character 4, Figs. 4–5, both lost in *C. fusius* according to our results). All seven species occur in the lowlands, unlike the previous lineage, but most are also found in montane habitats.

Cyanophrys berthae is the sister of the seven-species *C. herodotus* lineage in the successively weighted cladogram (Fig. 13), but in the equally weighted original most parsimonious trees, it was sometimes the sister of the five-species *C. longula* lineage. The genitalia of *C. berthae* are nearly identical to those of *C. amyntor*, but *C. berthae* shares frons color, androconial structure, and restriction to montane habitats with *C. longula* (Table 1).

Cyanophrys berthae has been proposed for "vulnerable" status (Brown 1993, Brown and Freitas 2000 and references therein, Otero et al. 2000) and listed as "almost threatened" (Mielke and Casagrande 2004). Its relatively basal position in the

cladogram increases its priority as a species of conservation concern (Atkinson 1989, Vane-Wright et al. 1991).

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- Brazil that we have examined are listed below (museum acronyms listed in Methods). If the elevation was not recorded on a specimen's data label, we parenthetically note the elevation for that site as it is listed in gazetteers. So far as we are aware, there are no other known specimens of *C. berthae*.
1. Minas Gerais, Barbacena, 900 m. 1 ♀ (Private collection of Karl Ebert, Santa Clara, São Paulo, Brazil); 1 ♀, 11 May 1969 (USNM); 1 ♀, 27 May 1986 (USNM).
 2. Minas Gerais, Poços de Caldas, 1,300–1,400 m. 1 ♂ and 1 ♀, March (Ebert).
 3. São Paulo, Serra do Japi, 1,050–1,250 m. 1 ♂, 24 March 1990 (USNM); 1 ♂, 25 March 1990 (USNM); 1 ♂, 14 May 1990 (USNM); 1 ♂, 2 June 1990 (USNM).
 4. Paraná, Curitiba, (934 m). 1 ♂, December 1945 (UFPR).
 5. Paraná, Ponta Grossa, (969 m). 1 ♀, March 1948 (UFPR).
 6. Paraná, Castro, (999 m). 1 ♀ (BMNH)
 7. Santa Catarina, Corupá, 19 October 1975. 1 ♀ (UFPR). (Corupá is located at 75 m elevation at the base of the mountains on the road leading to São Bento do Sul, a well-known butterfly locality above 800 m elevation that is the likely collection place for this specimen.)

APPENDIX

The data for the 13 museum specimens of *C. berthae* from 7 localities in southern